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DEMOGRAPHIC PATTERNS OF THE SHRUB CEANOTHUS MEGACARPUS IN AN OLD STAND OF CHAPARRAL IN THE SANTA MONICA MOUNTAINS

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ABSTRACT

Wildfires have had a major influence on the structural and functional adaptations that have evolved in Mediterranean-type ecosystems. Some chaparral shrubs sprout after fires while others produce serotinous cones or seeds refractory to germination until they are cued by a fire. Ceanothus megacarpus is a sclerophylous shrub commonly found in California in either pure or mixed stands which does not survive fires but whose seeds germinate following a fire. Because in recent decades man-made fires have become frequent, few older stands remain, and they have been described as "decadent" or "senescent." Since data on older chaparral stands are sparce, a stand of chaparral in the Santa Monica Mountains of southern California, which last burned in 1929, was studied in an effort to elucidate the survivorship patterns and community structure of Ceanothus megacarpus as it ages. Ceanothus is responsible for 68 percent of the basal coverage at this mixed stand, and one-eighth of the Ceanothus were found to be dead. Over 130 such dead individuals were cut at ground level and aged by ring counts to establish the survivorship curve for this species in this chaparral community in the absence of fires.

INTRODUCTION

Wildfires have had a major influence on the structural and functional adaptations that have evolved in species of Mediterranean-type ecosystems. In California chaparral for example, shrubs regenerate after fires from basal sprouts or seed germination cued to the first postfire season. Additional evidence of adaptation to fire is seen in the herbaceous and suffrutescent flora. These species are depauperate in mature chaparral but dominate in the first few years after fire.

Specialization to fire is seen in certain species of Ceanothus and Arctostaphylos. These shrubs produce abundant seed throughout their lifespan which lie dormant in the soil for many years until germination is stimulated by fire. These species lack the ability to resprout after fire and thus are often referred to as obligate seeding shrubs. In the absence of fire these species neither rejuvenate their canopy from basal sprouts as other sprouting shrubs do (see Keeley et al., this volume), nor do they recruit new seedlings.

The demographic patterns for one such species, Ceanothus megacarpus Nutt. has been well documented in studies by Schlesinger et al. (1982). This shrub is distributed on the coastal front of the Coast Ranges from Santa Barbara County to San Diego County, often forming nearly pure even aged stands dating back to the previous fire. As has been documented for other obligate seeding species, seedling populations are high in the first postfire year but nil in later years. Mortality in the first year for shrub seedling populations is typically quite high (Horton and Kraebel 1955, Keeley and Zedler 1978, Mills 1983). The causes of mortality are not clearly worked out although drought, predation and competition from the dense herbaceous vegetation are likely important. After the first year, mortality is relatively low during the first decade. However, as the shrub canopy closes in, Schlesinger and Gill (1978) found another sharp increase in mortality and they attributed this stand-thinning to increased competition for water (Schlesinger and Gill 1980).

After stand-thinning in the second decade, mortality in C. megacarpus was shown to taper off once again. Schlesinger's studies, however, did not extend beyond the second decade. It is not known what happens after this time. Anecdotal observations in the literature suggest that after approximately 30 to 40 years another sharp increase in mortality is to be expected due to stand "senescence."

The purpose of the present study was to extend Schlesinger's observations on C. megacarpus survivorship patterns to beyond the second decade. Although not abundant, patches of old chaparral do occur in the range of C. megacarpus. We studied a stand dominated by C. megacarpus and unburned for greater than 50 years.

STUDY SITE AND METHODS

Field observations throughout its range failed to uncover any stands of pure C. megacarpus older than approximately 30 years of age. However, a stand largely dominated by this species and 55 years of age (in 1984) was discovered along Pacific View Drive in the western section of the Santa Monica Mountains of Ventura County. It was a west facing slope of about 30 degree inclination at 380 m elevation.

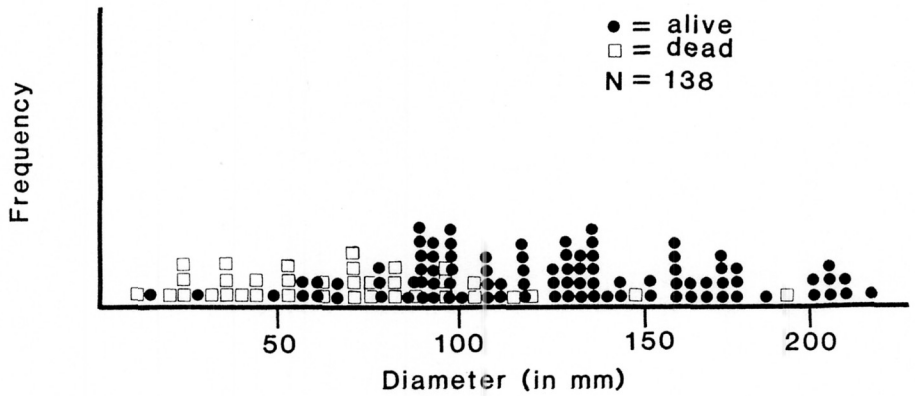
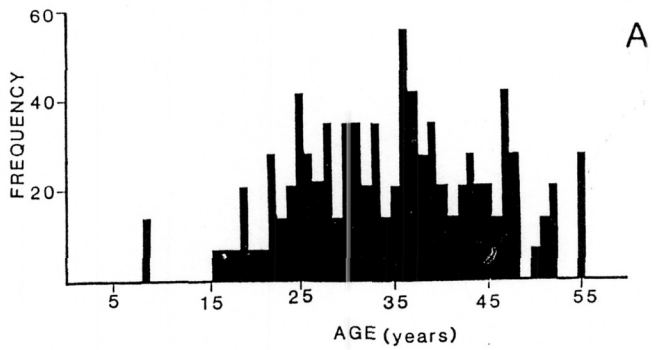


Figure 1

Distribution of diamters for dead and alive Ceanothus megacarpus shrubs encountered in the 45 2x4 m plots.



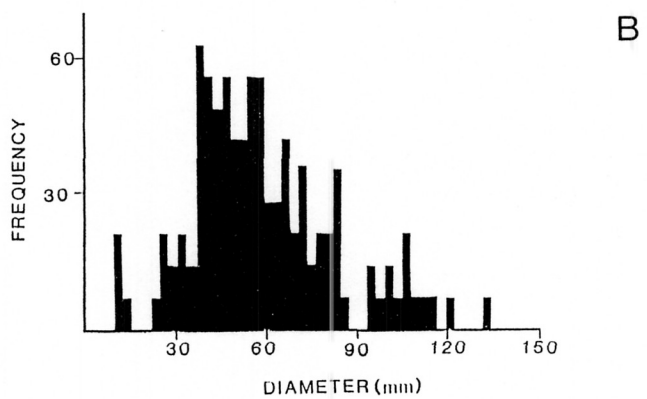


Figure 2

Distribution of ages (A) and diameters (B) for population of dead Ceanothus megacarpus shrubs n = 125).

Table 1

Community composition for the Ceanothus megacarpus dominated site in the Santa Monica Mountains of southern California.

Species		Basal Coverage (m^2/ha)	Density (#/ha) Stems	Density (#/ha) Plants	Frequency of Plants (%)
Ceanothus megacarpus	Alive	35.80	3000	2528	71
	Dead	5.00	1083	833	42
Adenostoma fasciculatum	Alive	4.85	1167	4167	44
	Dead	2.68	5417	333	47
Salvia mellifera	Alive	2.83	2972	1055	36
	Dead	4.13	4389	861	44
Cercocarpus betuloides	Alive	2.58	34,306	611	47
	Dead	0.66	5833	0	38
Quercus agrifolia	Alive	2.87	333	28	2
	Dead	0.17	111	0	2
Misc.	Alive	3.07	8941	3165	
	Dead	2.24	2249	306	
Total	Alive	52.01	50,719	11,637	
	Dead	14.79	18,971	2,333	

To characterize the stand, 45 2x4 m plots were laid out and the diameter of each stem was recorded. Survivorship patterns for C. megacarpus were determined in a manner similar to that used by Schlesinger and Gill (1978). Specifically, across an area of approximately 30x30 m all dead C. megacarpus were cut and a stem section at ground level was removed. As noted by Schlesinger and Gill (1978), we found that most standing dead shrubs were quite sound in spite of having been dead for as long as thirty years or more. Stems were subsequently recut, polished, aged by ring counts, and stem diameters were measured in our laboratory. Because of the highly convoluted shape of the stems, diameters were determined by taking the mean of two diameters measured at 90 degree angles from each other. A total of 130 dead plants were collected but only 125 are present in our data; partially rotted stems were discarded.

Schlesinger and Gill (1978) considered that their error of +/- one year on stems 10 to 15 years of age did not alter their conclusions. Replicate determinations in our laboratory indicated a similar accuracy in age determination and it is also unlikely to result in major alterations in our conclusions.

RESULTS AND DISCUSSION

C. megacarpus was responsible for about 70 percent of the basal coverage while the next most important species Adenostoma fasciculatum (chamise) covered about 10 percent (Table 1). Some of the other species found at the site were Salvia mellifera, Cercocarpus betuloides and Quercus agrifolia. The dead/alive ratio was 0.33 for C. megacarpus, indicating that two-thirds of the population was still alive.

Schlesinger and Gill (1978) had noted that in stands of approximately 10 to 20 years of age the variance to mean ratio for number of C. megacarpus plants per plot was greater for alive plus dead plants than for alive plants alone. They interpreted this to mean that during thinning, the population moved from a more clumped to a more random distribution. Such a comparison is shown in Table 3 for our site, indicating that this pattern is continuing in older stands as well. Schlesinger and Gill (1980) also found that mortality in young stands tended to be concentrated in the smaller plants. We found a similar trend in this old stand as seen in Figure 1.

Table 2

Comparison of ratios of dead/alive individuals for the dominant species at the Santa Monica site based on data in Table 1.

Species	Dead/Alive Ratio		
	Cover	Plants	Stems
Ceanothus megacarpus	0.14	0.33	0.36
Adenostoma fasciculatum	0.55	0.08	4.64
Salvia mellifera	1.46	0.82	1.48
Cercocarpus betuloides	0.26	0	0.17
Quercus agrifolia	0.06	0	0.33

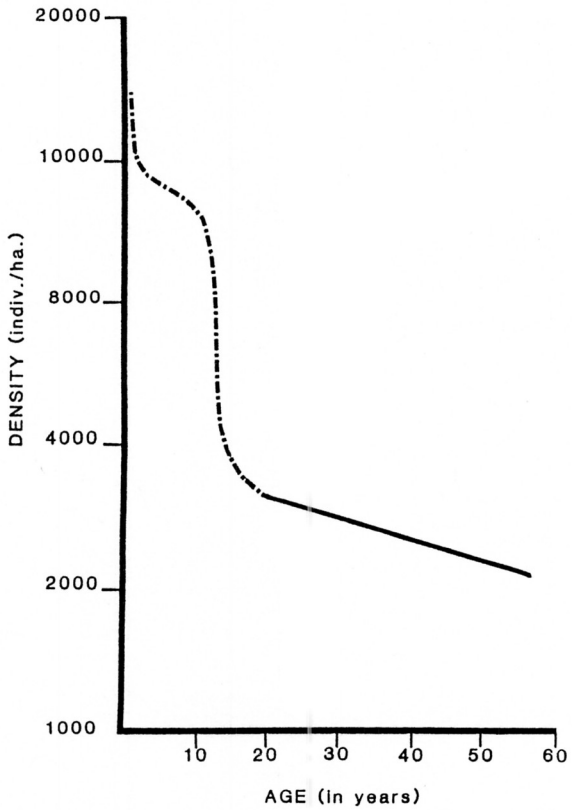


Figure 3

Estimated survivorship curve for the Ceanothus megacarpus population unburned for 55 years. The solid line indicates the survivorship of the population based on the observed mortality (Figure 2A). The dashed line was estimated by assuming a similar survivorship curve as documented by Schlesinger et al. (1982).

Table 3

Variance/mean ratio for the number of Ceanothus megacarpus plants per plot (n= 45 2x4 m plots). Alive plants indicate the present population and dead plus alive indicates the population at a previous point in time.

C. MEGACARPUS PER PLOT			
	$\bar{X}$	VARIANCE / MEAN	
DEAD + ALIVE	2.02	2.31	P 0.001
ALIVE	2.67	1.76	P 0.001

The age distribution for the dead C. megacarpus stems is shown in Figure 2A. We found very few dead stems less than approximately 20 years of age, undoubtedly due to deterioration of stems which died early on after fire. Mortality appears to have peaked at around 35 years of age and seems to have remained relatively constant over the past two decades. Figure 2B shows the distribution of stem diameters for the dead C. megacarpus population. While mortality appears to remain relatively constant with age, it is clear that smaller plants have a greater probability of dying than larger plants.

An estimated survivorship curve for this population is shown in Figure 3. The solid part of the curve shows changes over the past 25 years based on the density shown in Table 1 and the mortality rates shown in Figure 2A. Assuming a thinning curve observed by Schlesinger et al. (1982), we have extrapolated back to the time of the last fire. In this stand of ceanothus chaparral it appears that after the high mortality associated with stand thinning during the second decade, the population is slowly declining. Assuming mortality remains linear, projections into the future indicate that this stand of chaparral will be well over 100 years of age before C. megacarpus is completely eliminated.

CONCLUSIONS

Mortality of C. megacarpus shrubs in a 55-year old chaparral stand has remained relatively constant over the past 30 years.

The greater numbers of dead individuals in the smaller size classes as well as the greater numbers of large alive plants suggest that mortality in C. megacarpus is related more to intraspecific competition than to a programmed mortality due to senescence.

The notion of senescence or decadence as it relates to older stands of obligate seeding chaparral species needs to be reevaluated or at least defined more clearly in the light of the evidence offered by this study.

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